Why Are Male Hawks So Small?

For birds that eat birds, life is tough; this might explain why, unlike much of the rest of the avian world, females are bigger than males

In the majority of bird species males are larger than their mates. A number of arguments have been brought to bear on this, prominent among which is that competition between males for access to females is responsible for their greater bulk: in other words, it is a manifestation of sexual selection.

In birds of prey, however, the usual pattern is reversed: females are larger than males, sometimes substantially so. Attempts to explain the cause of this "reversed" size dimorphism draw much less consensus among researchers, with the result that there is a proliferation of hypotheses in the literature. In a recent survey of this controversial topic Helmut Mueller of the University of North Carolina counted more than 20 (*1*). These various hypotheses generally can be assigned to one of three major categories of explanation: behavioral, sex role differences, and ecological.

In recent years arguments that incorporate some element of ecological influence have been gaining popularity among theorists, but, as always with questions of an essentially historical nature, they have remained recalcitrant to experimental proof. One recent paper on the subject, by Ethan Temeles of the University of California, Davis, offers an extension of certain ecological hypotheses and indicates directions in which tests might proceed (*2*).

The issue of size dimorphism among birds of prey is in fact two questions in one. The first concerns the reason why females are consistently bigger than males, a fact that has been known since medieval times among those whose pleasures involved hawking or falconry. The second relates to a correlation between type of diet and degree of dimorphism: the extent of size difference between females and their mates increases as diet moves through carrion, insects, fish, mammals to birds. Put crudely, this amounts to a simple formula: the faster the prey moves, the greater will be the size dimorphism in the pursuers. This observation has been clearly formulated only in recent times, although several authors have made some reference to it since the early 1970's (*3*).

The very striking link between diet and size dimorphism sets a trap for those who would seek to understand its origin, says Ian Newton of the Institute of Terrestrial Ecology, Monks Wood, England. Because so much of the biology of birds correlates with their diet in some way, there will be many factors that also correlate with the size dimorphism but may not be causative of it. Great cautiousness is required, warns Newton. Furthermore, many of the explanations advanced so far can be argued cogently for the extremes of dimorphism but begin to fail at the margins.

In his recent review of current hypotheses, Mueller concluded that a behavioral explanation is most reasonable, specifically the female dominance hypothesis. Originally formulated in the 1960's by Tom Cade of Cornell University, and recently revived by Susan Smith of Mount Holyoke College, and now by Mueller, the idea centers on something of a protection mechanism for the females, which enhances pair-bonding and pair-bond maintenance.

Peregrine falcon

Females are 50 percent heavier than males in this bird-eating species.

In nonpredatory birds, in which the male may be physically and behaviorally dominant to the female, courtship often involves something of a role reversal, with the male offering food morsels to the female. For predatory birds, armed as they are with dangerous talons, beaks, and instincts, social interactions are potentially hazardous, even during courting, it is argued. A female that is larger and more dominant than its mate is simply a safer bird. If females were consistently to choose mates that are smaller than themselves, then the reverse dimorphism observed among predatory birds would emerge. In addition, it would explain the correlation between type of diet and degree of reverse dimorphism: predatory skills would have to be more keenly honed among birds that kill other birds than those that live on carrion or insects, and thus would be potentially more of a threat to their mates, the argument runs.

This hypothesis is of course an aspect of sexual selection, through female choice. It has the obvious attraction of casting both the direction of size dimorphism and the correlation with diet in one explanation. Mueller points out that biologists generally have little hesitation in adducing sexual selection to explain size dimorphism when males are bigger than females, but seem constrained to search for explanations among other phenomena—specifically ecological phenomena in this case—when females dwarf the males.

Newton is unconvinced by the female dominance hypothesis, because it does not explain why the small males do not suffer the same fate from which the females are supposed to be escaping. Moreover, Cade himself has shown with experimental pairings of males and females from different races of American kestrels, designed so that males were the larger of the couple, that violence did not break out against the females.

There are other possibilities in the realm of sexual selection, none of which has been thoroughly tested as yet. For instance, if small males were better equipped for hunting, then female choice for this talent would produce the observed pattern of size dimorphism. Or, if small body size were important in aerial competition for females, again the observed pattern might be produced.

Unlike the female dominance idea, the ecological and sex role hypotheses tend to be only partial explanations and are therefore often interlinked. For instance, the basis of the ecological explanation is that birds of prey constantly face a threat of food shortage, which is alleviated if the two sexes are foraging for prey of different sizes and are therefore not in competition with each other. Known as resource, or niche, partitioning, this strategy would be particularly critical during the fledgling period when food shortages are worst and are keenly felt.

This reduction in foraging competition would be achieved by having one sex larger than the other, but by itself it does not dictate which of the two should be the bigger.

Sex role hypotheses generally assign reproductive advantages to the female in having a large body size. Obvious possibilities include being able to produce more eggs per clutch and, through accumulating substantial stores of body fat and protein, being vigilant at the nest throughout incubation and early brooding. Indeed, Newton and his colleagues have shown that, in sparrow hawks, reproductive success is determined by the reserves the female is able to accumulate prior to laying (*4*).

Although it becomes something of a circular argument, there is clearly some sense for a female that is becoming heavy with food reserves to refrain from foraging immediately prior to and during incubation and brooding, which is what happens in the great majority of predatory birds. Some birds in this condition simply sit almost motionless at their nests, looking for all the world as if they are sick, says Richard Reynolds of the Rocky Mountain Forest Range Experimental Station, Colorado. Add to this argument the risks involved in the nature of the foraging in these birds—the chase, the fight, the kill—and the reasons for a gravid female remaining at the nest and eschewing the hunt become compelling.

With the female withdrawing from foraging for the incubation and brooding period, which is sometimes a substantial part of the year, the role of the male is to collect food for his mate and the chicks as well as for himself. Why should this make him smaller than the female?

The abundance of avian prey drops off rapidly with increase in size, and so there would be benefits in foraging in as small a prey size range as possible. But the greater agility of small birds demands a closer match in body size between prey and predator. Hence there would be potential selection for small males in bird-eating birds. The argument becomes

Hunting success

Birds that prey on birds may reap less energy per unit time because each hunt has a low likelihood of success.

weaker with the decreasing agility of the prey, which might explain the match between diet type and degree of size dimorphism. A less conventional answer is that the males have remained the same size as their ancestral stock, and the females have increased in size to maximize their reproductive functions.

In his recent paper Temeles suggests an approach, based on optimal foraging theory, that might help discriminate between the strictly ecological and the conventional sex role division hypotheses. If males and females are of different body sizes in order to eliminate competition between the sexes, their net energy return would be higher than in two birds of the same size, even though neither may be at the foraging optimum. Compare this to the conventional sex role division hypothesis. Here the male is expected to be at a foraging optimum whereas the female would not be. Two birds of the size of the male would be close to maximum foraging efficiency. Collecting reliable data to test foraging efficiency is different enough in birds, but in species whose home range sometimes exceeds 12 square miles the problems are horrendous. Still, in principle, these are testable questions and therefore have merit in a topic where many are not.

At its simplest the ecological hypothesis says that degree of size dimorphism correlates with diet in the way described earlier, because the abundance of prey items decreases from carrion to birds, hence the competition between the sexes becomes stiffer, and hence the selection pressure for the two sexes to be of different sizes is greater. Several authors modified this notion somewhat by pointing out that the agility of prey items increases through this spectrum (*5*). This has the effect of narrowing the size range of prey that can be taken as agility increases. Hence competition is once again honed, because the abundance of prey is effectively reduced.

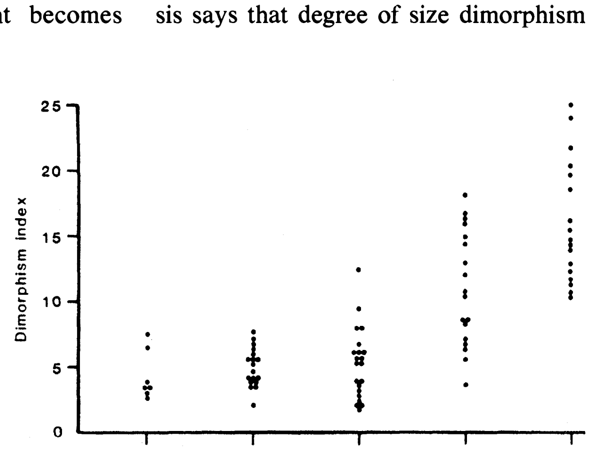
Temeles points out that greater agility of prey not only narrows the potential size range that a predator can exploit, but it also reduces the likely success during each hunting exploit. In a survey of data on raptors he found that hunting success did indeed vary according to the nature of prey items, showing a decline across the prey spectrum mentioned earlier. Hunting success is as follows: for invertebrates, 82.0 percent; fish, 58.0 percent; mammals, 22.95 percent; birds, 12.95 percent.

The energy return per unit time for a predator in pursuit of a prey of a particular calorific value is therefore less if that prey is a bird than if it is a fish. Predators feeding at the bird and mammal end of the prey spectrum will therefore have to spend more time foraging than those at the fish and insect end. In addition, they might be forced to spend time foraging outside their optimum prey size range. Both these factors serve to sharpen potential food competition between the sexes, and hence widen the size gap between the sexes.

Temeles's concept, which he terms the prey vulnerability hypothesis, does not by itself explain why it is that the females are always bigger than the males. This hypothesis, like most of the ecological hypotheses, has to link in with some aspect of division of sex roles, in which females gain a reproductive advantage in being as large as possible. As Newton notes, most biologists now agree that reproductive advantage is part of the equation somewhere: the differences come in where the major emphasis is placed.—**ROGER LEWIN**

Diet correlates with dimorphism

The relationship seems simple: the faster the prey moves, the more developed the size dimorphism is in the predator.



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